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Sardine cycles, krill declines, and locust plagues: revisiting 'wasp-waist' food webs

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'Wasp-waist' systems are dominated by a mid trophic-level species that is thought to exert top-down control on its food and bottom-up control on its predators. Sardines, anchovy, and Antarctic krill are suggested examples, and here we use locusts to explore whether the wasp-waist concept also applies on land. These examples also display the traits of mobile aggregations and dietary diversity, which help to reduce the foraging footprint from their large, localised biomasses. This suggests that top-down control on their food operates at local aggregation scales and not at wider scales suggested by the original definition of wasp-waist. With this modification, the wasp-waist framework can cross-fertilise marine and terrestrial approaches, revealing how seemingly disparate but economically important systems operate.

Top-down, bottom-up, and wasp-waist controls on the food web

The relative importance of predation from upper trophic levels ('top-down control') and resource availability at the food web base ('bottom-up control') in structuring ecosystems is a topic of lively debate [1]. Many ecologists suggest that bottom-up controls are the norm with top-down the exception, most prevalent in food webs that are simple, perturbed, fresh water, or benthic [2]. The marine literature has also generated the concept of a third ecosystem state, known as 'wasp-waist' [3]. These systems are suggested to have just one or two biomass-dominant species at mid-trophic levels that channel most of the energy flow. Such species are proposed to exert 'middle out' control; that is, top-down control over trophic levels below them and bottom-up control over levels above them [3,4]. Other suggested wasp-waist traits include schooling and large population fluctuations that are driven by climate variabil-

ity. Small planktivorous fish (anchovy and sardine) were first considered as wasp-waist species, but the term has now expanded in the marine literature to include other fish [5], Antarctic krill [4,6], and even pelagic amphipods [7].

The term 'wasp-waist' has not yet been considered in the context of terrestrial systems. However, there are some intriguing parallels here between land and sea; locusts, for example, have been described as 'strongly interacting species' [8]. Similar to their marine wasp-waist counterparts, locusts also display dramatic population increases and huge, organised aggregations that impact their predators and prey alike. Can we expand the wasp-waist concept to include terrestrial as well as marine systems?

In this article, we argue that large-scale top-down control from a species at the wasp-waist is unlikely, but after this modification in definition, it provides a framework to understand a series of economically important systems. By comparing the shared traits of species occupying the wasp's waist, we can better understand how they achieve such high biomasses, and exchange promising approaches to their study and management. Despite a chorus of opinion that this type of marine–terrestrial cross-fertilisation would be beneficial [2,9], it is still conspicuous by its absence. We use the wasp-waist concept as a specific, concrete example of the benefits of this type of exchange.

Sardines, krill, and locusts: the value of comparative approaches

What could a mid-latitude fish, a polar crustacean, and an insect pest have in common? Many aspects of their biology, including their trophic level, are fundamentally different (Table 1). Here, we emphasise instead the parallels between these disparate species to highlight how they can fit into a common wasp-waist food web topology. Sardines, anchovies, Antarctic krill, and locusts share great economic importance and an enormous study literature. However, the study approaches differ radically. Most locust studies are autecological, for example on physiology, sensory biology, polyphenism, swarming, feeding, or pest control [10];

Table 1. Expression of 'wasp-waist' traits by sardine, anchovy, Antarctic krill, and locusts, with avenues for the cross-exchange of concepts between systems

Traits	Sardine and anchovy	Antarctic krill	Locusts	Potential transfer of insights and approaches
High maximum biomass	~200 t fresh mass km^{-2} [23]	~150 t fresh mass km^{-2} [13]	~160 t fresh mass km^{-2} based on [8,48]	Marine studies have emphasised total biomass and biomass density, locust studies have emphasised the area occupied by plagues, and the two need to be combined for a better appreciation of their role in the wider food web
Climate-driven population fluctuations	Decadal or multidecadal cycles of sardine and anchovy (Box 1, main text) but no clear alternation [17] despite different ecological niches; populations sensitive to climatic variability [e.g. El Niño–Southern Oscillation (ENSO) and upwelling strength] [3,14,15,66]	Intense interannual and decadal variability (Box 1, main text); salp populations can also cycle dramatically in the habitat of krill, but this is not a species alternation [30]; linked to climatic variability (ENSO and sea ice extent) [13,20,67]	Recession periods punctuated by plagues lasting several years (Box 1, main text); these are controlled by rainfall and temperature-related bottom-up factors [16,22]	Fishery-type approaches, such as stock recruitment curves, could be applied more widely
				Parallel work being done to tease out the drivers of population dynamics based on time series; approaches here can also transfer
				Some of the caveats to predicting future populations by extrapolating present-day drivers [11,21] could be applied to krill
Migration and population dispersal	Spawning migrations and expansion of range during high biomass periods, with isolated spawning pockets when biomass low [23].	Population dispersal via large-scale advection [13], with evidence for off-shelf spawning migration and debated evidence of autumn southwards migration [25]	Range expansion of desert locusts from 'recession' areas to larger dispersal areas, with swarms capable of migrating thousands of km [22]	Locust migration and sensory biology studies are well advanced [51] and the concepts have wider application to marine species
				The concept of range expansion and contraction could be applied to krill, exploring habitat preferences and density dependence in the context of available habitat [23]
Bottom-up control on its predators	Modelling and time-series analysis show a degree of bottom-up control on predators [14,15,31]	Breeding success of several krill predator species decreases during periodic poor krill years [13,68]	Transient but important food item for many trans-Saharan migrant birds [8]	Marine approaches (e.g., measuring biomass and rate processes in multiple trophic levels, mass balance approaches, and end-to-end food-web modelling) can be applied to understand how locusts fit into the wider food web [12,13,32])
Top-down control on its food	Only clearly evident at small (<5 km) scales [40]	Small-scale effects of grazing impact [39] and nutrient regeneration [26,33]; at larger scales, krill–food relations are positive [25]	Extensive damage to crops and natural vegetation [8]	Important but under-researched area for all of these taxa; as outlined above, terrestrial studies could benefit by transferring marine grazing and nutrient regeneration approaches. This includes their role in pulsed events [58] and in the spatial transfer of nutrients and consumable protein between systems [13]
Aggregation	Schooling is key to their ecology, with schools having similar volume:area ratios [38] and internal profiles of packing density to those of krill [69]	Forms dense schools typically 10–100 m across but occasionally 'superswarms' of >1 million t [38]	Overcrowding of solitary phase leads to the swarming phase with traits such as better disease resistance [70] and the selection of plants whose toxins guard locust against predation	Work on swarming is more advanced in locusts [10,50] and some of the models have wider relevance.
				Difficulties in experimenting on schooling species have led a wide suite of '*in situ*' approaches [34,49,71], which could be developed in swarming terrestrial invertebrates
Diverse diet and flexible food processing	Food size (estimated) ranges from approximately 10 μm to 2000 μm for sardines, with larger food (>10 mm) available to the more raptorial anchovies; higher absorption efficiency of nitrogen than of carbon [53–55]	Food size (estimated) range is approximately 3–3000 μm [42,57]; variable food processing and absorption [72] preferential nitrogen over carbon absorption [58,71]	Swarming desert locusts are generalist feeders on grasses, shrubs, and trees; flexible food processing minimises excesses or deficits in protein and/or carbohydrates [56]	Diet and post-ingestion processing are fundamental processes, still poorly understood [56]; their parameterisation strongly determines the outcome of marine ecosystem and biogeochemical models [12,32]; better marine–terrestrial exchange of concepts and approaches could help in this difficult field
Importance to humans	Anchovy and sardines comprise approximately 25% of the global fish catch; management has been based on a longer history of high fishing pressure than it has for krill [4]	One of the few large fisheries in the world with scope for expansion; this has recently been occurring and the fishery is now worth US$241 million annually [68]	Plagues have provided economic catastrophes throughout history; in 2004, US$71 million was spent mainly on control measures involving massive insecticide doses in Africa [8]	Approaches to management of these species can cross-fertilise, for example through 'ecosystem approaches', modelling dependent species as well as the target species (see 'Bottom-up control on its predators'); management approaches being developed for krill [64] could benefit from the longer history of sardine and anchovy fishery management

research on planktivorous fish often emphasises schooling dynamics and fisheries-relevant issues as well as the food web [11,12], whereas krill research tends to be more food-web based [6,13].

Despite these differences, the species all achieve enormously high biomass densities at mid-trophic levels, with unusually large variability in population size on timescales from interannual to multidecadal. Two other suggested wasp-waist traits are more ambiguous concepts and these have been contested [14,15]. The first gives wasp-waist its name: the dominance of just one (or two) species at the low-diversity midriff of the food web. Second is the purported middle-out control on the rest of the food web. Here, we broaden the outlook to include other commonalities, such as aggregation and nutrition. Table 1 summarises some key aspects of these taxa and promising avenues for cross-system exchange of study approaches and concepts.

Boom and bust population dynamics

The relation between locust outbreaks and climatic indices represents an approximately 2000-year time series, documented in the rich Chinese literature [16]. Fluctuations in anchovy and sardine abundance are evident even in the fossil record [17], whereas isotopic approaches suggest major changes in krill on century–millennial timescales [18,19]. Numbers of all species fluctuate, so what is different about these 'wasp-waist' species? Box 1 illustrates the great extent of the variation we see in these species. For example, the large fluctuations in krill stocks, coupled to their rapidly warming habitat and potential for fisheries expansion, have driven efforts to project future trajectories [6,13,20]. An important caveat has been identified independently within the locust and fisheries management literature; the factors governing population dynamics often change as the climate shifts [11,21], so that the longer-term drivers may be totally different to those at present.

The population explosions in sardine, anchovy, and locusts coincide not only with increased numerical densities across the home range, but also an expansion of the range or migration to new home ranges [22–24]. The mechanisms by which these occur clearly differ between species, with the associated density-induced phase changes in locusts being the best studied [10]. By contrast, the dominant paradigm in the krill literature is advective flux from 'source regions' to areas of downstream expatriation [13]. However, within the wasp-waist context, the concepts of migration [25] and horizontal and vertical range expansion [26] could also be tested (Box 1).

How do we define top-down control?

The roles of top-down and bottom-up controls on the food web are hotly debated for a variety of reasons. They are scale dependent and sensitive to precisely how we define the evidence for top-down control. At the largest scales, the case for bottom-up control is clear; climate dictates where on the planet the tropical rainforest belts lie and fishery yields at global and regional scales are largely predictable from new primary production [27]. At the scale of large marine surveys, top-down control tends to be inferred from observations of negative interannual correlations between successive trophic levels [3–5,28]. However, there is a suite of problems with inferring control from such correlations, of which attributing causation from a correlation is just one [29].

Exactly how we define the evidence for top-down control is clearly fundamental. For example, at interannual- and mesoscales, negative relations found between krill and copepods or krill and salps have been interpreted variously as a predator–prey, competitive, or non-interactions. The latter explanation was simple and equally plausible: some regimes favour krill and others favour the other taxa [30]. Likewise, correlation-based evidence for top-down control by small fish on their zooplankton food [3] has since been questioned [14].

Given these problems of correlation and causation, we suggest that the current shorthand for inferring top-down control from negative correlations needs stronger rate process-based support. Does most of the energy from primary production go through the wasp-waist species or via other pathways? If it is through the wasp-waist, then a strong top-down control is possible. Food-web models for anchovy and sardines in upwelling systems showed that, despite their high biomass, they channel only a minority of the energy [14,15,31]. A similar situation applies for krill (Figure 1).

We could not find comparable assessments of the extent of top-down control in locusts. This testifies a more fundamental imbalance between the approaches in marine and terrestrial ecology. Mass balance, biogeochemical, and whole-food web modelling is more advanced in the sea, whereas on land, the research tends to be more autecological or at least more bottom-up orientated [9]. This is paradoxical; land plants are often large, immobile and slow growing, and their grazers are more easily observable, albeit sometimes ephemeral. In a 3D ocean, there is an array of problems simply of sampling the plethora of drifting or swimming grazers and their food, before even trying to measure their grazing impact. Nevertheless, marine scientists have tackled these issues, with a growing interest in end-to-end food-web models [12,32]. This is a prime area where terrestrial ecologists could learn from their marine colleagues to better understand the role of key consumers in the food web.

Top-down control, as defined above, refers to an animal grazing down its food. However, due to the aggregations and high biomasses of wasp-waist species, they can also affect lower trophic levels through pulsed nutrient regeneration. Of the species compared, only krill has attracted much attention for this biogeochemical role. This includes importing, exporting, or recycling pulses of carbon, nitrogen, and iron [26,33]. Such topics are surprisingly neglected in planktivorous fish [34] and locusts [35,36], but their effects could be likened to stochastic perturbations. Thus, in some respects, locust outbreaks could be compared to fire, where adapted systems rely on the periodic local-scale perturbation to maintain productivity and diversity in the longer term. Learning how such pulsed regeneration processes work is another area that would benefit from better terrestrial–marine cross-fertilisation of approaches.

Fundamental to the ecology of planktivorous fish, krill, and locusts is their tendency to form large schools or

Box 1. Great population fluctuations in wasp-waist species: the importance of time- and space scales

For desert locusts, anchovy, sardine, and possibly Antarctic krill, the large fluctuations in total population size reflect increases not only in mean density within the home range, but also in the total range. With ranges spanning a few tens of million km² during such population explosions, coupled to highly aggregated distributions, assessing changes in total population size and their drivers is nontrivial. Figure I illustrates time series available for Japanese sardine, Antarctic krill, and desert locust during the past century, based on contrasting sampling approaches. Japanese sardine data refer to the total biomass of the spawning stock, desert locust data reflect number of 1° grid squares infested with locust swarms, whereas krill data reflect mean densities (of juveniles plus spawning stock) in surveys located mainly within its population centre. If the population increases and/or decreases for all of these species indeed reflect range expansion and/or contraction coupled to increased and/or decreased densities within the main population centre, then the time series in Figure I might even underestimate the degree of variability. In any case, their abundance indices varied by several orders of magnitude throughout the available time series. We selected a key, biomass dominant, lower trophic-level copepod (*Calanus helgolandicus*) as a yardstick by which to gauge this level of variability. Based on standardised sampling at a single site, *C. helgolandicus* varied only approximately fourfold, with populations maintained within this range, despite the rapid warming within the north-east Atlantic area.

Just as large-scale spatial patterns in the populations need to be incorporated when determining time trends, spatial extent of environmental features can also act as driving variables. For example, the biomass of small pelagic fish has been related to the size of the upwelling habitat from year to year [44] and indices of winter ice area relate to krill abundance in the subsequent summer [67]. With better areal coverage of locust swarm distribution and climatic data, spatial analyses are integral to modelling time-series data on locust plagues [22]. Regardless of the indices used, the major interannual and decadal scale fluctuations in krill, anchovy, sardine, and locust populations seem to be under strong bottom-up control, sensitive to various climatic correlates, such as rainfall, temperature, and the El Niño–Southern Oscillation cycle [16,20,66]. Such scales of variability are superimposed on trends over longer timescales, reflecting regime changes and human intervention, such as pest control or overfishing of small pelagic fish.
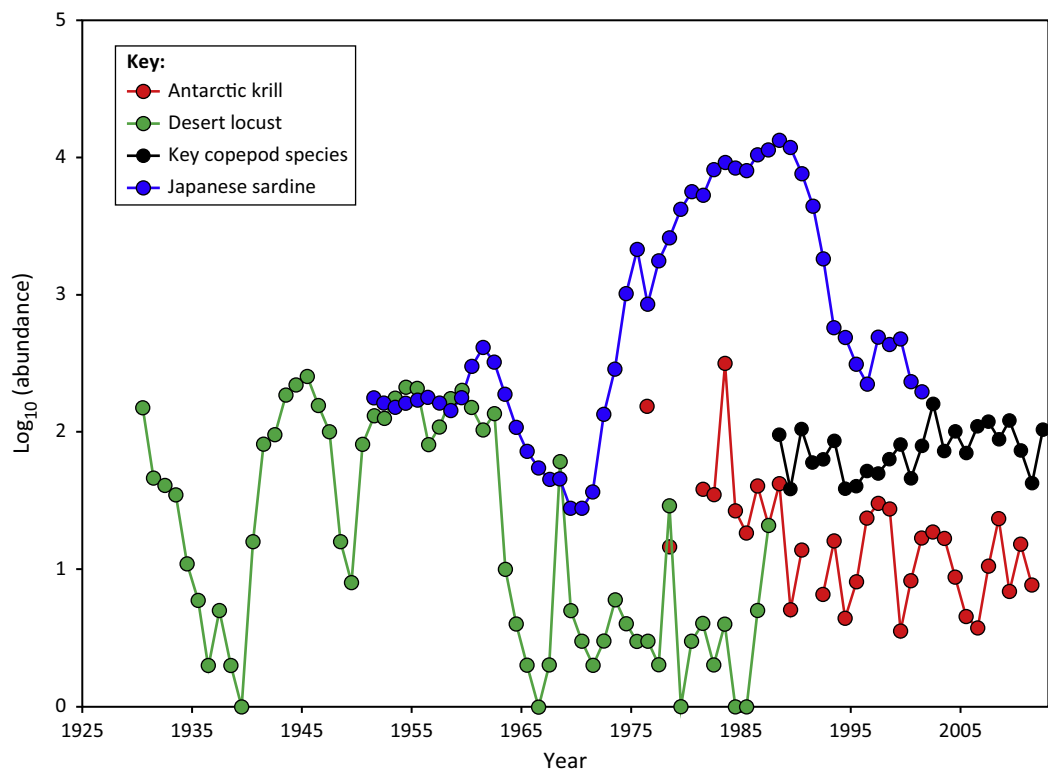
Figure I. Great fluctuations in population sizes are seen in wasp-waist type species; here we compare them on a log (× +1) scale with a key copepod with high biomass that is not wasp-waist (*Calanus helgolandicus*). Japanese sardine (*Sardinops melanosctictus)* spawning stock biomass is illustrated in thousands of tonnes from 1951 to 2001 (data from [73]); Antarctic krill (*Euphausia superba*) postlarval abundances (no. m⁻²) are from the updated KRILLBASE database (www.iced.ac.uk/science/krillbase.htm) [25,67]. We selected only data from nets of 1-m diameter or larger, sampling within 10°E to 90°W from within the season November April inclusive, yielding 6669 stations in the sampling era 1976–2011. Desert locust (*Schistocerca gregaria*) data were transcribed and replotted as annual averages from the monthly values in Figure 2 from [22]. They represent the number of 1° grid squares infested with desert locusts swarms from 1930 to 1987. *Calanus helgolandicu*s data refer to annual means for all copepodites (CI-CVI, no. m⁻³, 2168 net hauls) recorded from the Plymouth L4 time series station in the Western English Channel (http://www.westernchannelobservatory.org.uk/).

swarms. Aggregation is a process with shared costs and benefits across a range of terrestrial and aquatic organisms, so there is much understanding that spans the land–sea divide [37]. Given that feeding and aggregation are intimately linked, this is the scale at which we now examine the concept of top-down control.

Aggregation and large-scale top-down control are hard to reconcile

Overgrazing leading to food depletion is a commonly cited downside of being in an aggregation, along with oxygen depletion in aquatic systems [37]. For example, schools of planktivorous fish and krill, despite being variable in size,
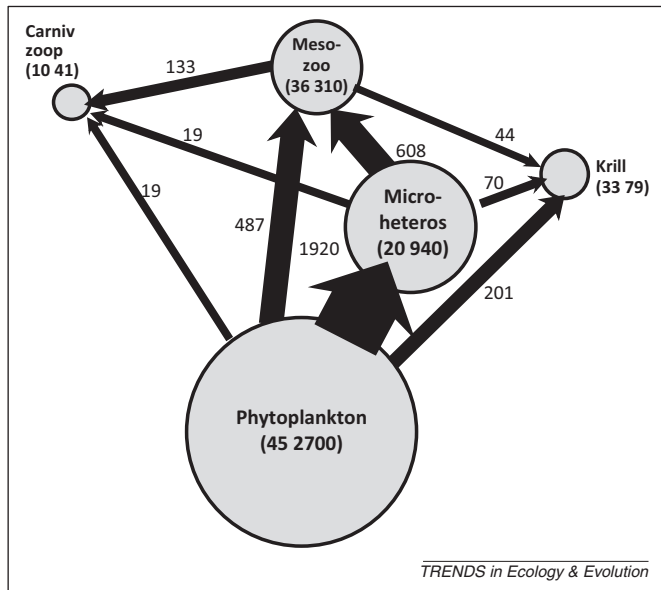
Figure 1. Energy flows through the major planktonic functional groups at South Georgia, where krill biomass densities are among the highest. Data are from a balanced Ecopath model [68], updated with revised values of krill diet [42]. Arrows widths are scaled to energy flows, which are labelled, with units of consumption in tonnes fresh mass km^2 year^{-1}. The biomass of each functional group (tonnes fresh mass km^{-2}, i.e., g fresh mass m^{-2}) is presented, followed by the production of the group (tonnes fresh mass km^{-2} y^{-1}). Bubble sizes reflect the relative production of the group. This model pertains to multiyear average biomasses over the South Georgia shelf and shows the relatively low role of krill in energy flow in this system, despite it containing among the highest krill densities in Antarctica [13,25].

share a remarkably consistent ratio of surface area to volume of ~3.3 m^{-1} [38]. This has been interpreted as the optimal trade-off between predator avoidance and resource acquisition [38]. At small scales (10s of km^2), negative relations between small pelagic fish and zooplankton, or krill and phytoplankton, suggest that individual schools do impact on their food [39,40]. The serious local damage of locust swarms to foliage is more graphically visible on land. It is unclear whether this reflects greater top-down control (possibly related to the slower growth rates of terrestrial plants [2]), or whether it is better documented because of the economic consequences; perhaps both.

However, for krill at least, the impact is not as severe as one might expect. Even in the areas of exceptionally high krill concentrations (approximately 100 g C m^{-2}), Chlorophyll *a* concentrations did not drop below 0.5 mg Chl *a* m^{-3} [39], which is above the half-saturation value for krill growth [41]. The corollary of this is the absence of severe food limitation of schooling krill, supported by the high gut fullness and growth rates of krill caught from schools [41,42]. There are presumably mechanisms that reduce overgrazing in these schooling species. Likewise in desert locusts, phase change and migration are direct responses to living at high population density with associated depletion of resources and cannibalism [43]. We argue that, if an aggregating species did indeed exert top-down control sufficient to cause a large-scale, interannual negative relation with its food, then at the scale of an aggregation, this impact must be amplified by orders of magnitude. In other words, the individuals would be in a perpetual state of food deprivation or nutrient imbalance.

From this line of reasoning, we suggest that these aggregating species do not fit the concept of large-scale

top-down control from a wasp-waist, but rather the reverse: by lightening their foraging footprint, they reduce food limitation, allowing high stock densities (Table 1). Clearly, density dependence must become an issue above a certain threshold [44]; for example egg, cannibalism is significant in Peruvian anchovy at high densities [45], but evidently the threshold for this becoming a significant control is high. Indeed, the ability to support these exceptional animal densities without severe density-dependent effects is probably essential for a 'boom and bust' population dynamic to work. The question is: how do they do it?

Finding enough food within an aggregation

Behaviour within aggregations is hard to study, especially in aquatic environments. Therefore, this field is particularly ripe for methods, insights, and models to transcend the respective research communities. For example, parallels appear between krill and planktivorous fish in school structure (Table 1). Insights into feeding dynamics could cross the land–sea divide, for instance to test the hypothesis that feeding is a benefit and not a penalty for aggregation. Possible advantages include more effective foraging as a result of information sharing and 'group intelligence' or with the energy savings due to joint movement (the 'peloton' effect) [46].

For these reasons, aggregations are often described loosely as 'superorganisms', whose density can satiate predators and that collectively can have enhanced ability to sense predators or gradients in food [47]. Whether our wasp-waist examples also benefit from these various advantages is only speculated upon; observing and measuring rates within dense aggregations is difficult [46,48]. Here, some of the techniques being refined to measure '*in situ*' growth rates of schooling krill [49] could be transferred to other species. Growth can be used as an index of the overall net benefit accrued to an organism, so could be compared, for example, between aggregating and non-swarming individuals or species, or according to swarm size. Conversely, some approaches are more advanced on land, such as modelling and tracking aggregations [50], and these could be transferred to the sea. Likewise, approaches taken in locust sensory biology could be considered in marine species, for example to test potential navigation mechanisms [51]. 'Cannibalism within the lifeboat' of migratory locust swarms is another example of an individual-level response to local food depletion [43] that might repay investigation in marine species.

Dietary diversity is a further unifying feature of sardine, anchovy, Antarctic krill, and at least some locusts, for example the desert locust. The implications of a broad diet have often not been interpreted in this wider sense, perhaps because previous terrestrial–aquatic comparisons emphasise the fundamental differences at the base of the food web [9], with poorly size-structured terrestrial systems contrasting with size-structured aquatic assemblages of filter feeders that have no terrestrial counterpart [2]. However, at a more basic level, the parallels remain. The desert locust in its swarming phase is a generalist feeder on grass, shrubs, and trees [52]. Likewise, schooling krill, anchovy, and sardines are also great generalists; flexible dual feeders using both suspension and raptorial
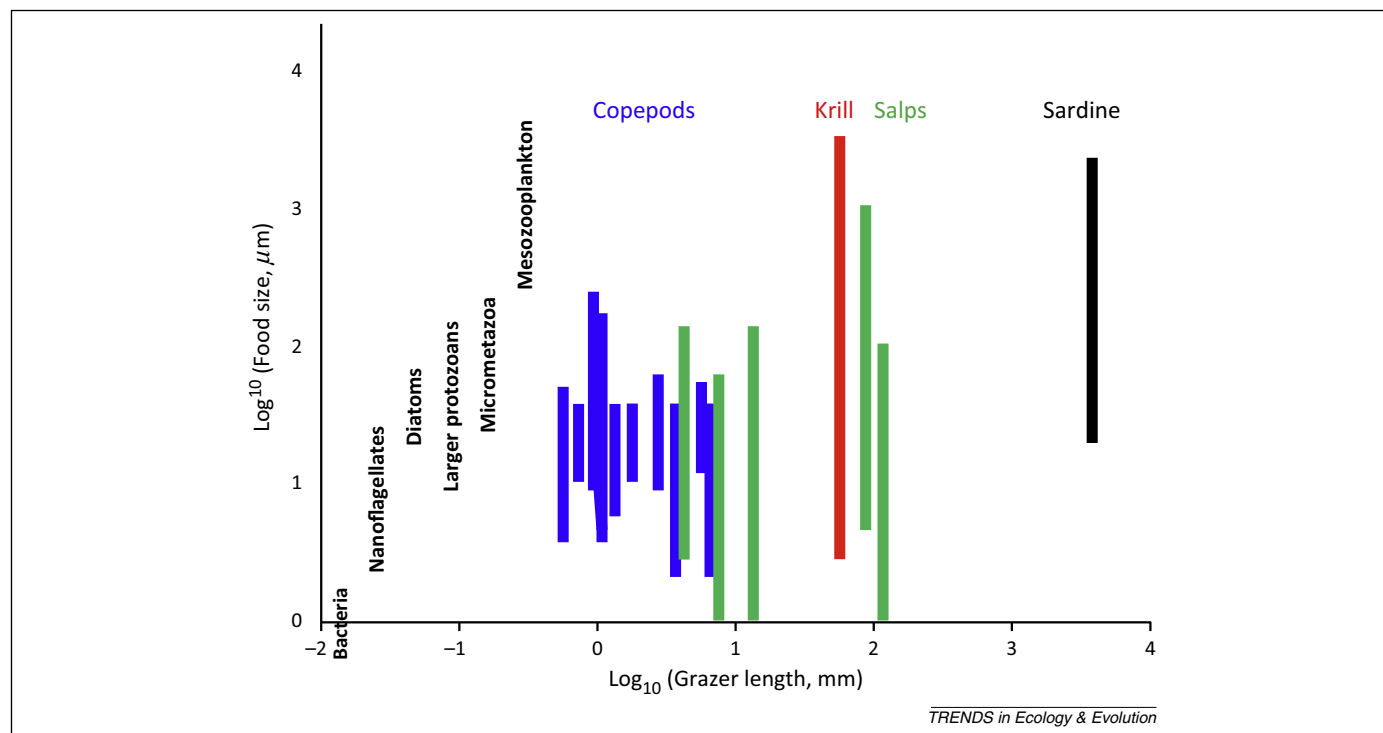
Figure 2. Food-size spectra (equivalent spherical diameters) of filter-feeding copepod species (blue bars) salps (green), *Euphausia superba* (red), and sardine (black), all in relation to maximum body length of the grazer. Vertical text refers to the typical size ranges of the major prey functional groups. These comprise overlapping trophic levels, classified for example as protists versus metazoans. Metazoans are also classified on size, with micrometazoa (e.g., early larvae of small copepods) passing a 200-μm mesh and the larger mesozooplankton retained. Copepod and salp (gelatinous tunicate) data are from [74] and Appendix S1 of [72]. Krill data are from [42,57]. Sardine (*Sardina pilchardus*) data are from [55] and references therein. Anchovy are not illustrated alongside these primarily filter feeders due to the greater incidence of raptorial feeding and, consequently, larger prey items. However, similar to sardine, their available prey-size spectrum spans well over two orders of magnitude [53].

feeding modes to include an exceptionally wide dietary diversity [42,53–55].

Filter feeding is not unique to planktivorous fish and krill, but Figure 2 shows just how wide their prey size spectrum is, compared with other major planktonic filterers. This provides access to food spanning at least three trophic levels. A drawback of filter feeding is the ability of larger motile prey to sense and escape [27]. However, it might be impossible to escape a massed array of filters of an advancing sardine or krill school [46,54]. Does the school, rather than the individual, then form the effective net size? Regardless of how they do it, these planktivores can eat their main competitor for phytoplankton (microheterotrophs) as well as tap into an even larger source (copepods) that reflects a longer-term buffer of stored energy.

This broad-brush discussion of commonalities between disparate taxa should not obscure some critical differences in detail at the species level. For example, unlike the desert locust, a generalist feeder, the migratory locust *Locusta gregaria* is a specialist on grasses [56]. Nutritional adaptation to a single, abundant resource base may obviate the need for dietary diversity in this species. Likewise, anchovies have a narrower food spectrum compared with sardines, relying more on raptorial capture of larger zooplankters [53–55]. These details in ecology of coexisting species are germane to our understanding of how they interact, whether as predator and prey, as competitors, or through differences in resource requirements [30]. Indeed, there are other candidate wasp-waist-type species, such as wildebeest, elk, or buffalo, each having a unique biology.

Although the mechanisms of ingestion are completely different between these aquatic and terrestrial species, the basic processes underlying nutrition are similar. They must absorb a sufficient array and balance of macro- and micronutrients, based on a diet that is often deficient in some but with excess of others. Here, the concepts emerging after years of controlled study of insect nutrition could be translated to their pelagic schooling counterparts, which are harder to study without containment-induced artefacts [42,57]. Insects can compensate for nutrient dilution by increasing the amount of food that they process [56]. Furthemore, the swarming phenotype of desert locusts has wider dietary diversity compared with the solitary phase [52,56], reflecting greater behavioural and physiological flexibility. Comparing whether food processing is more flexible with broader diets and with grazers that aggregate [58], as done for insects [56], would help to test whether this is an adaptation to nutrient shortage or imbalance. The challenge is to understand how species-level processes (as emphasised in terrestrial studies) map onto wider ecological function (as championed in marine studies)

Managing these species with a more holistic approach
An expanding human population and climate change, coupled to marine fisheries overexploitation and terrestrial food and water shortages, are pressing issues for global food security [59,60]. Exploiting small, highly nutritious, 'wasp-waist'-type organisms lower in the food chain has several advantages, including their high biomass and turnover rates plus aggregations that facilitate harvesting

[12,61,62]. However, a series of economic, cultural, and technical issues has tended to impede this exploitation. The marine species are generally used to produce meal for animal feed, whereas the consumption of terrestrial insects (which can also be a mechanism for pest control) is largely confined to developing countries [60,62]. Whether as a food source or for pest control, the need to understand how wasp-waist-type food webs operate is a prerequisite for their management.

Depending on whether you are a farmer or a fisherman, the ability of locusts, anchovy, sardine, or krill to bounce back from low population sizes is either a curse or a blessing. Either way, their economic importance in terms of fisheries revenue or pest control costs is already measured in hundreds of millions of dollars per year (Table 1). All of these species have critical roles in structuring their food webs and need to be managed as such. The Committee for the Conservation of Antarctic Living Resources (CCAMLR), which is responsible for managing Antarctic krill fisheries, has adopted a form of 'ecosystem-based management', whereby attention is paid to the state of krill predators as well as to the krill stocks themselves [63]. The importance of krill or forage fish to a wide suite of predators is obvious [13–15]. By contrast, the management of locusts focusses on their impact on crops, but their wider role in the food web is a research area that could draw from marine modelling approaches. For example, the Sahel region supports a range of threatened or declining trans-Saharan migrant bird species that depend on locusts as food and are affected by pesticide eradication measures [8]. Together with the other effects from pesticides, this has been used to argue for other forms of control measures [8].

Perhaps one of the key differences in the future management of marine and terrestrial wasp-waist species is that the potential exists for large-scale farming of terrestrial insects [62], whereas fishing is the only feasible method to exploit anchovy, sardine, and krill. The Antarctic krill fishery is one of the few major fisheries with scope for further sustainable expansion [59]. Mindful of the sensitivity of krill to a changing climate [6], CCAMLR are starting to develop a feedback management approach that could adjust catch limits in response to variations in climatic drivers [64]. This process is at an early stage, so could benefit from lessons learnt from the longer history of anchovy and sardine fishery.

Labels such as 'keystone', 'wasp-waist' (from the marine), or 'strongly interacting' (from the terrestrial) are simplifications and they tend to lose their specific meanings over time. However, the label should not assign systems with traits that they do not have. For example, a food web with 'wasp-waist' topology (*sensu* [3]) has different behaviour to others, such as greater potential for instability arising from changes at mid-trophic levels [65]. With the caveat that the large-scale top-down control element is unlikely, the wasp-waist framework remains useful to help understand how seemingly disparate systems function. Equally important, probing the similarities and not just the differences between land and sea allows principles, ideas, and methods to flow across the communication barriers that exist between these disciplines.

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